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Diversification and Biogeography of the One-Toed Horses *Onohippidium* and *Hippidion*

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Abstract

In this report we describe a large sample of *Onohippidium galushai*, new species, from the Late Hemphillian (Early Pliocene) of western Arizona, one ramus of *Hippidion* sp. from the Early Hemphillian (Late Miocene) of the Texas High Plains, and one ramus of cf. *Hippidion* sp. from the Irvingtonian (Late Pliocene to Early Pleistocene) of southern California. These one-toed horses were previously thought to have been confined to Plio-Pleistocene deposits of South America. *Onohippidium* from Arizona possesses a retracted nasal notch, deep preorbital facial fossae, and dental pattern diagnostic of South American representatives of this genus. *Hippidion* from Texas and California exhibit the dental characters, especially in the deep ectoflexids, seen in South American representatives of this genus. This is the first report of these horses from North America. The presence of *Onohippidium* and *Hippidion* in North America demonstrates that diversification of these "endemics" occurred prior to dispersal to South America during the Pleistocene great faunal interchange.

Introduction

One of the most interesting groups of fossil horses is known from Plio-Pleistocene deposits of South America. These horses, which include *Hippidion*, *Onohippidium*, and *Parahipparion*, are, so far as is known, characterized by unusual morphological adaptations. Both *Hippidion* and *Onohippidium* have retracted nasal notches (Fig. 1). Along with this retraction, the nasal bones remain elongate and unreduced "splints." Some other mammals, such as tapirs, have retracted nasal regions; which is an adaptation to the presence of a proboscis. Retracted nasals

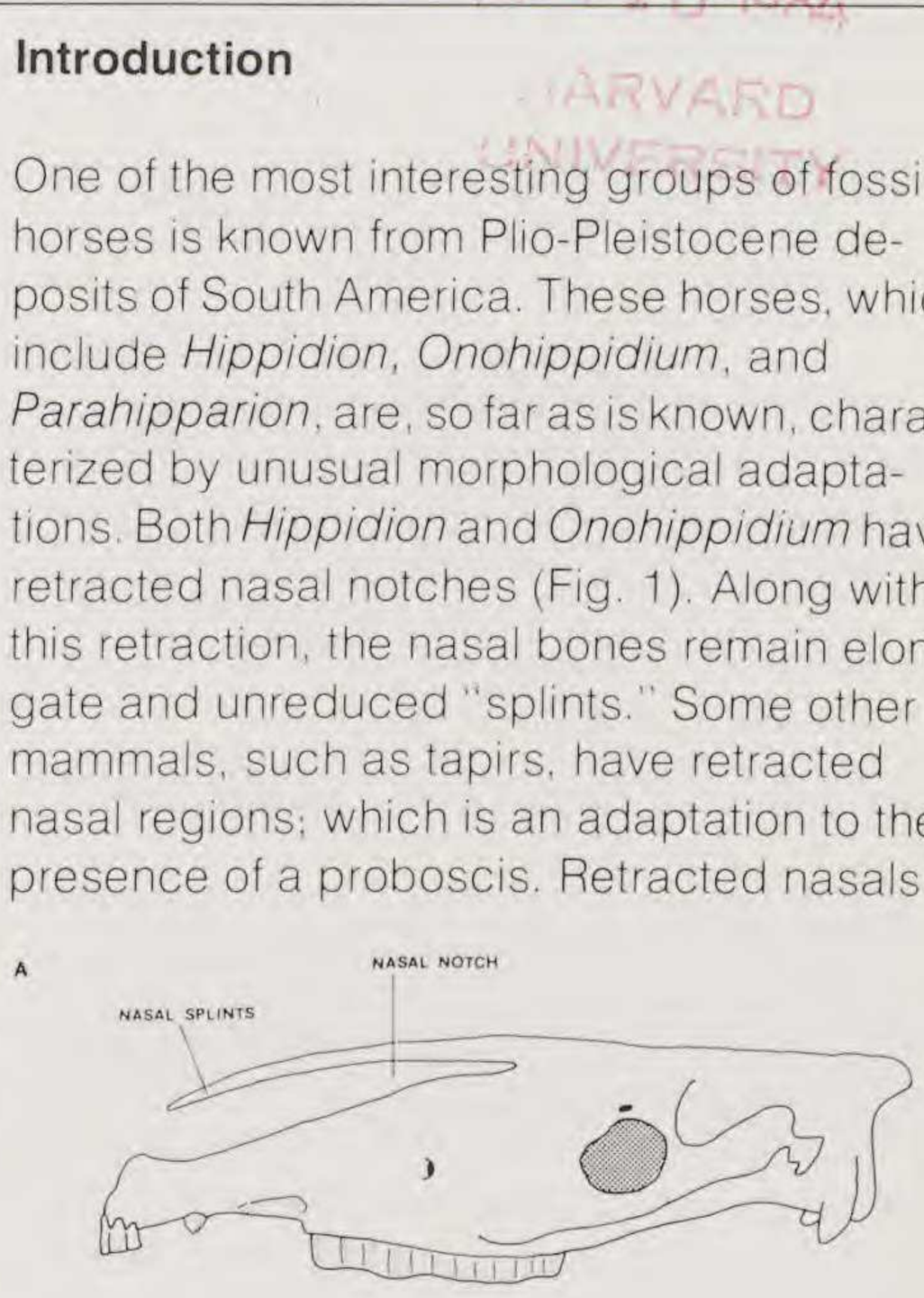
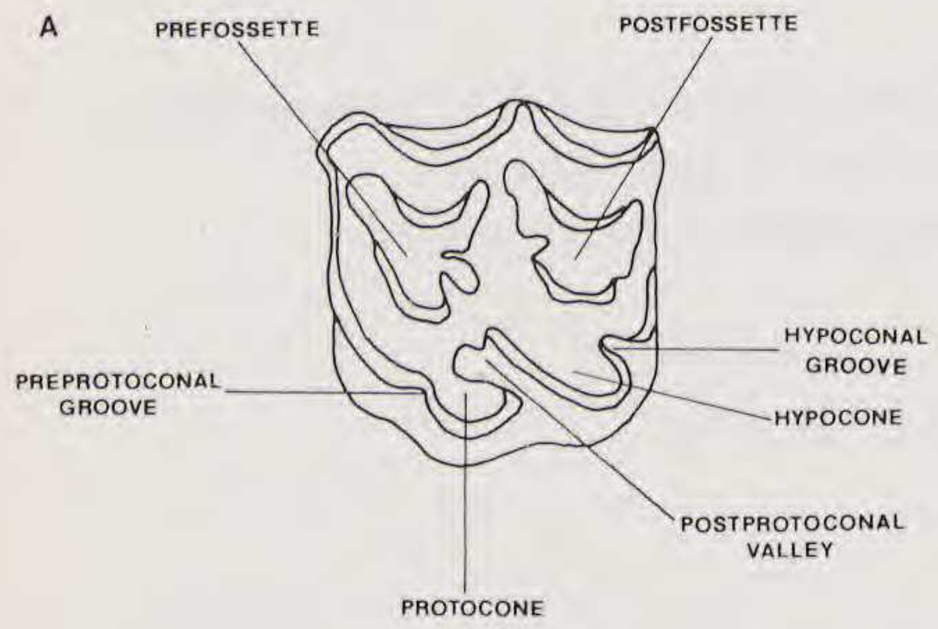


Fig. 1.
Skulls of *Hippidion (A)* and *Onohippidium (B)* showing characters discussed in text (adapted from Burmeister, 1875, and Sefve, 1912, respectively). The nasal splints in the *Onohippidium* specimen are broken anteriorly. Not to scale.



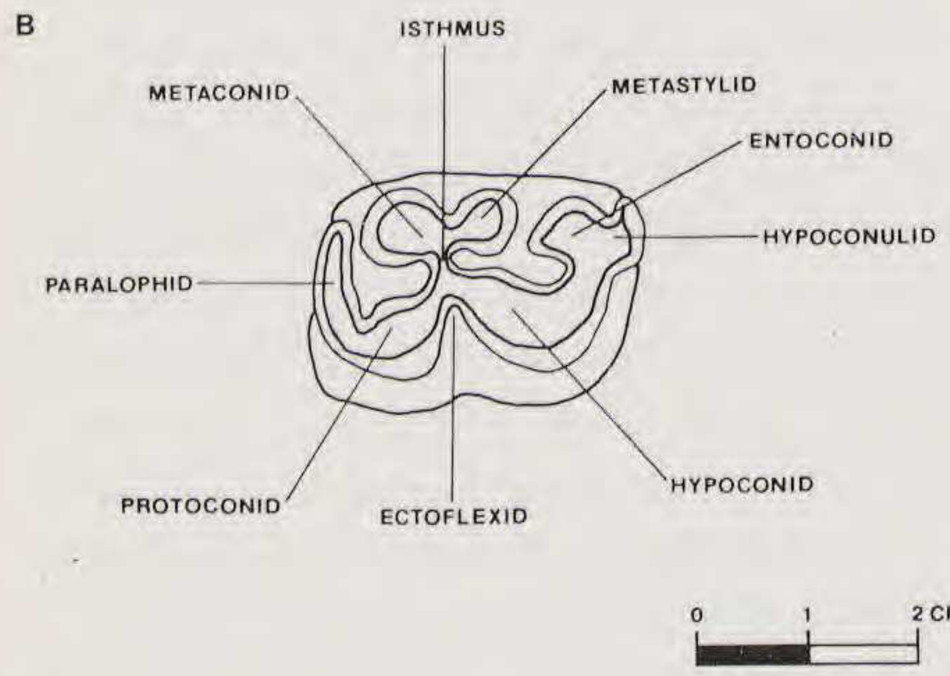


Fig. 2.
Left upper *(A)* and left lower *(B)* cheek teeth of a one-toed horse showing characters discussed in text. Nomenclature follows Stirton (1941), Skinner and Taylor (1967), and Skinner (MS).

are rare in fossil horses, although this feature has been described for certain *"Hipparion"* from Eurasia which apparently possessed a tapir-like proboscis during life (e.g., Sefve, 1927; Forstén, 1968; Sondaar, 1971). The only other reported occurrence of nasal modification in horses is in *Onohippidium* and *Hippidion*. The type of nasal modification seen in these two genera has not been observed in other horses. It is possible that these horses did not possess a proboscis because: 1) The nasal bones are not posteriorly retracted as seen in other mammals with a proboscis; 2) The elongate nasal splints would have restricted movement of soft anatomical structures. Simpson (1951, p. 147–148) states that: "The nasal bones [in *Hippidion*] . . . must have been well supported by a nasal septum of cartilage and other tissues. . . ." It seems that this type of nasal modification is related to olfaction, but a more specific function is not certain.

It is generally stated that *Onohippidium* and *Hippidion* were derived from a group of one-toed horses from North America (e.g., Matthew, 1924; Stirton, 1940). The purpose of this report is to describe the first-known record of these two genera in Hemphillian and Irvingtonian deposits of North America and to discuss their biogeographic significance.

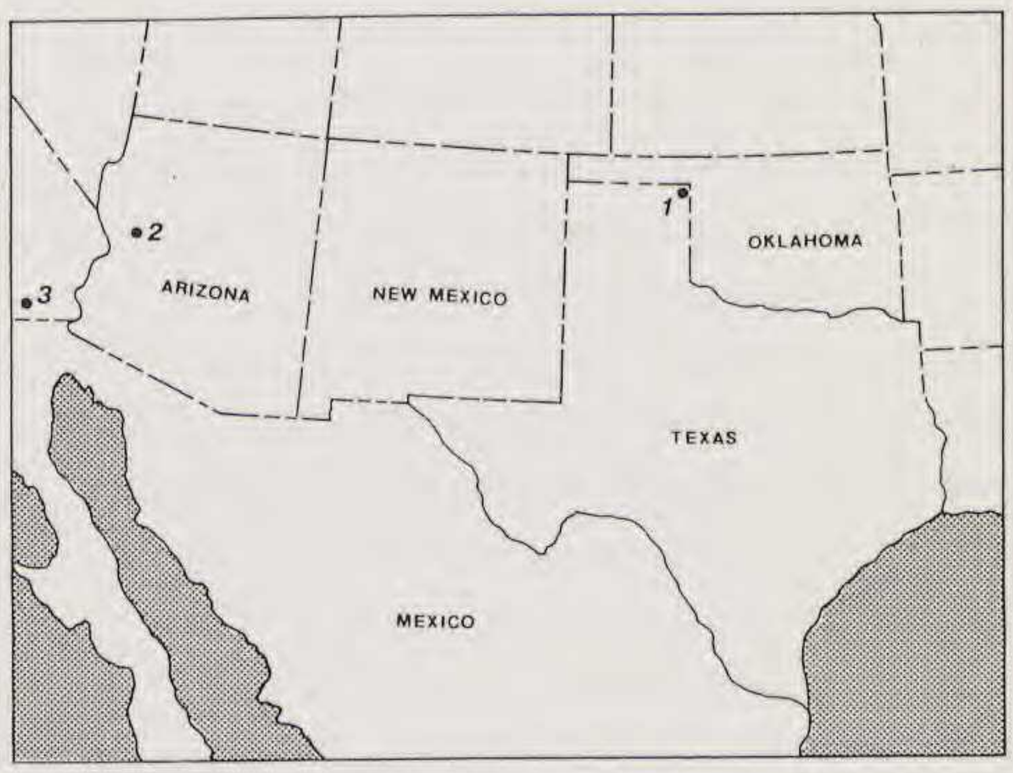


Fig. 3.
Fossil localities discussed in this report. *1*. Undescribed local fauna, unnamed rocks of the Ogallala Group, Early Hemphillian (Late Miocene) of the Texas Panhandle. *2*. Wikieup local fauna (l.f.), Big Sandy Formation, Late Hemphillian (Early Pliocene) of western Arizona. *3*. Sediments probably equivalent in age to the Vallecito Creek l.f., Irvingtonian (Late Pliocene-Early Pleistocene) of the Anza-Borrego State Park of southern California.

Abbreviations

The following institutions are referred to in the text:

F:AM	Frick: American Mammals, Department of Vertebrate Paleontology, The American Museum of Natural History
LACM	Section of Vertebrate Paleontology, Los Angeles County Museum of Natural History

All measurements of specimens are in millimeters and are abbreviated as follows:

A–P	Greatest anterior-posterior length
T	Greatest transverse width (labial-lingual; external-internal)
R	Right side of tooth row
L	Left side of tooth row
@	Measurement approximate

The dental nomenclature used in this paper and illustrated in Figure 2 follows Stirton (1941), Skinner and Taylor (1967), and Skinner (MS).

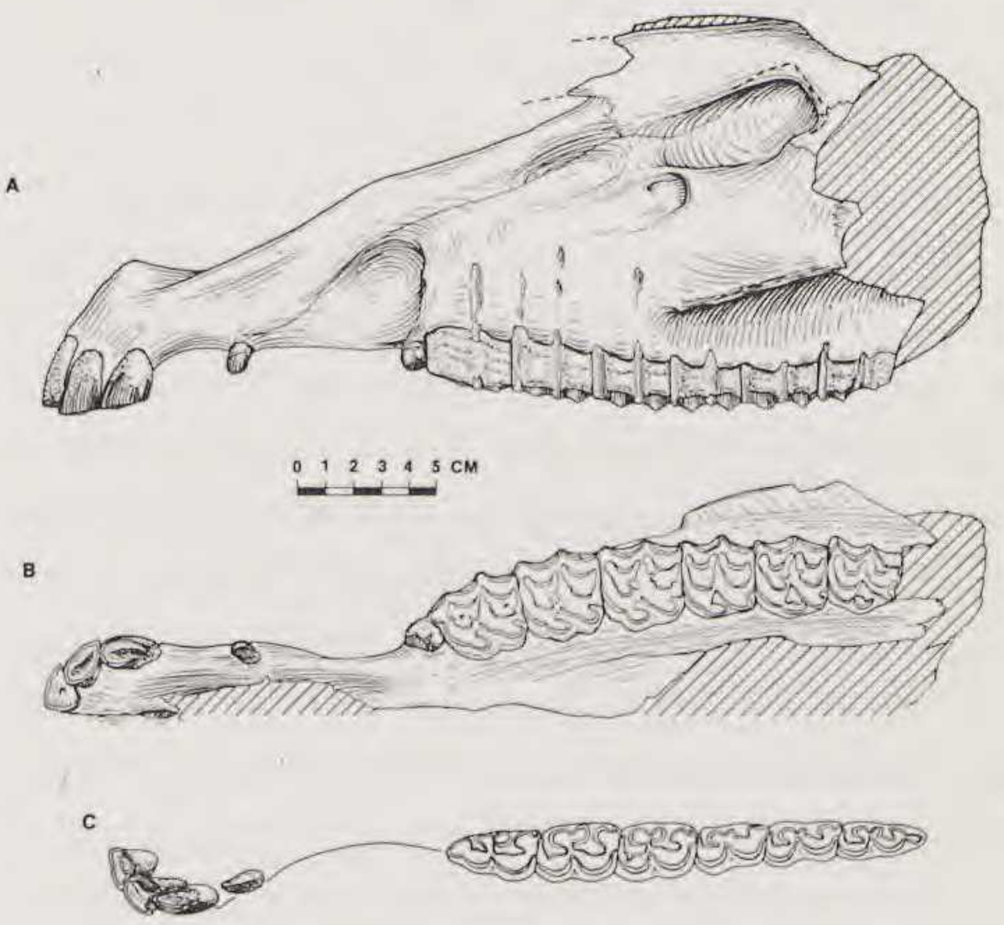


Fig. 4.
Onohippidium galushai, new species, from the Late Hemphillian of Arizona. *A*. F:AM 100077, holotype, left lateral view of partial skull. *B*. F:AM 100077, holotype, left upper dentition. *C*. F:AM 100078, right lower dentition, reversed.

Systematic Paleontology

Class **Mammalia** Linnaeus, 1758
Order **Perissodactyla** Owen, 1848
Family **Equidae** Gray, 1821
Genus ***Onohippidium*** Moreno, 1891

Revised Distribution. Early Pliocene (Late Hemphillian) of Arizona and Late Pliocene and Pleistocene of South America (Sefve, 1912; Hoffstetter, 1952; Webb, 1976; this report).
Generic Diagnosis. Horse with nasal notch that lies as far anterior as P^3–P^4 and as far posterior as the orbit. Nasal bones not retracted and remain elongate splints. Well-developed dorsal lacrimal fossa and no ventral malar fossa. Incisors with cement-filled cups (infidibula). Protocone oval to rounded with weak preprotoconal groove and well-developed postprotoconal valley. Lower cheek teeth with either shallow ectoflexids (externomedial valleys) and isthmuses in the permanent premolars or deep ectoflexids in the deciduous premolars and molars. Very simple enamel plications. Monodactyl metapodials.

Onohippidium galushai, new species
Fig. 4.

Pliohippus sp., Lindsay and Tessman, 1974, p.6.
Holotype. F:AM 100077, partial skull with well-preserved dentition.
Hypodigm. Hundreds of specimens, which consist of skulls, jaws, dentitions, and postcranials in the F:AM collection. There are specimens possibly referable to this species in other institutions, such as the small collections from the same locality at the University of Arizona Laboratory of Paleontology, but these were not examined during the present research.
Locality and Age. Frick field crews collected the F:AM specimens during the 1950s from the Big Sandy Formation of Mohave County, Arizona (Fig. 3). This formation, which consists of lacustrine clay to marginal sand facies deposited in an enclosed basin, outcrops along the Big Sandy River from approximately 8.5 km north to 12 km south of the town of Wikieup. Sheppard and Gude (1972) present a detailed stratigraphic description of this formation. Frick field crews collected a few specimens from washes north of Wikieup, but the bulk was collected from a locality approx-

imately 12 km south of Wikieup, near the southern outcrop margin. This locality is included in Sheppard and Gude's (1972, p. 6) reference section R-3 located ". . . along a wash that parallels Signal Road about 2,600 ft northwest of the road, from NW¼NW¼SW¼ sec. 29 to NE¼SE¼NW¼ sec. 29, T. 15 N., R. 12 W., Greenwood Peak quad." The fossil-bearing zone is located in the upper part of reference section R-3 (Sheppard and Gude, 1972; Galusha, MS). Galusha (MS) terms this zone the "Clay Bank Quarry locality," which is used in a broad sense to include fossils collected locally within this zone. One large concentration within this locality is approximately 125 m west of Clay Bank Quarry and is termed "Bird Bone Quarry." This fossil-bearing locality and zone can be relocated with the use of Frick field notes (Galusha, MS), Sheppard and Gude (1972), and the U.S. Geological Survey 7½' Greenwood Peak quad. During the falls of 1976 and 1977 MacFadden and Dr. Noye M. Johnson (Dartmouth College) relocated the Clay Bank Quarry locality and collected samples for paleomagnetic and fission-track analysis.

The mammalian assemblage from the Big Sandy Formation is informally termed the Wikieup local fauna (l.f.) in Tedford et al. (in press). A preliminary faunal list for specimens collected by the University of Arizona field crews is presented by Lindsay and Tessman (1974). The Wikieup l.f. is largely undescribed although some comparisons with assemblages of similar age have been made (e.g., MacFadden, 1977; Tedford et al., in press). Tedford et al. (in press) consider the age of the Wikieup l.f. to be Late Hemphillian (Early Pliocene), which corresponds to an absolute time interval of approximately 4 to 5 million years ago.

Etymology. Named in honor of members of the Frick Laboratory, Theodore and Marian Galusha.

Specific Diagnosis. Same as for genus with the following distinctions: Nasal notch retracted to above P^3–P^4. Fossa between buccinator and lacrimal fossae not as well developed as other *Onohippidium* (Fig. 4).

Description. The nasal notch is retracted posteriorly to a position which lies over P^3–P^4 and is intermediate between the conditions seen in North American *Pliohippus* and *Dinohippus* and in South American *Hippidion* and *Onohippidium*

There is a well-developed complex of fossae on the cheek. The buccinator fossa is anteriormost and in front of the cheek-tooth row. Posterodorsal to the buccinator fossa there is a faint preorbital depression; this is better developed in South American *Onohippidium*. Posterior to this faint preorbital depression there is a deep and well-defined lacrimal fossa that is also seen in South American *Onohippidium*. The infraorbital foramen lies above P^4–M^1.

The upper dentition of *O. galushai* is very similar to South American *Onohippidium*. The incisors have cement-filled cups. P^1 is reduced in size. The premolars are larger in cross section than the molars. The protocone is rounded to oval with a weak preprotoconal groove and a deep postprotoconal valley. Occasionally, especially in the molars, the protocone unites with the metaloph and hypocone forming a cement-filled enclosure. The hypocone is oval and usually slightly smaller than the protocone and there is a distinct posterolateral hypoconal groove. The pre- and postfossettes (lakes) are cresent-shaped. The plications on the fossettes are absent except for the posterior border of the prefossette and anterior border of the postfossette.

The lower incisors have cement-filled cups. The P_1 and its alveolus are absent, which is characteristic of advanced horses. The premolars are usually larger than the molars. The deciduous premolars show relatively deep ectoflexids, between the protoconid and hypoconid; however, these ectoflexids are not deep enough to divide the isthmus that connects the metaconid and metastylid to the protoconid and hypoconid, respectively. The permanent premolars have relatively shallow ectoflexids that do not divide the isthmus. The

enamel pattern is simple with few secondary plications.

Discussion. The retracted nasal notch with unreduced nasal splints, configuration of preorbital fossae, and, to a lesser extent, simple dental pattern provide convincing evidence for relating *O. galushai* to the South American representatives of this genus. So far as is known, *Onohippidium* has not been identified elsewhere in North America. Other contemporaneous horses for which skulls are known, i.e., *Pliohippus* and *Dinohippus*, have characters different from those seen in *Onohippidium*. *Pliohippus* has a different configuration of preorbital fossae and no retracted nasal notch, whereas *Dinohippus* has a simple preorbital area and no retracted nasal notch. There are numerous forms of the *Pliohippus-Dinohippus* complex for which the preorbital and nasal areas are not known. Therefore, it would be most satisfying if the *Pliohippus-Dinohippus* complex could be differentiated from North American *Onohippidium* solely on the basis of dentition. If this dental differentiation were possible, then *Onohippidium* might be identified at other Late Hemphillian North American localities. However, the dentitions of these contemporaneous forms are so similar, and there is so much variation within "populations," that generic differentiation on this basis is virtually impossible.

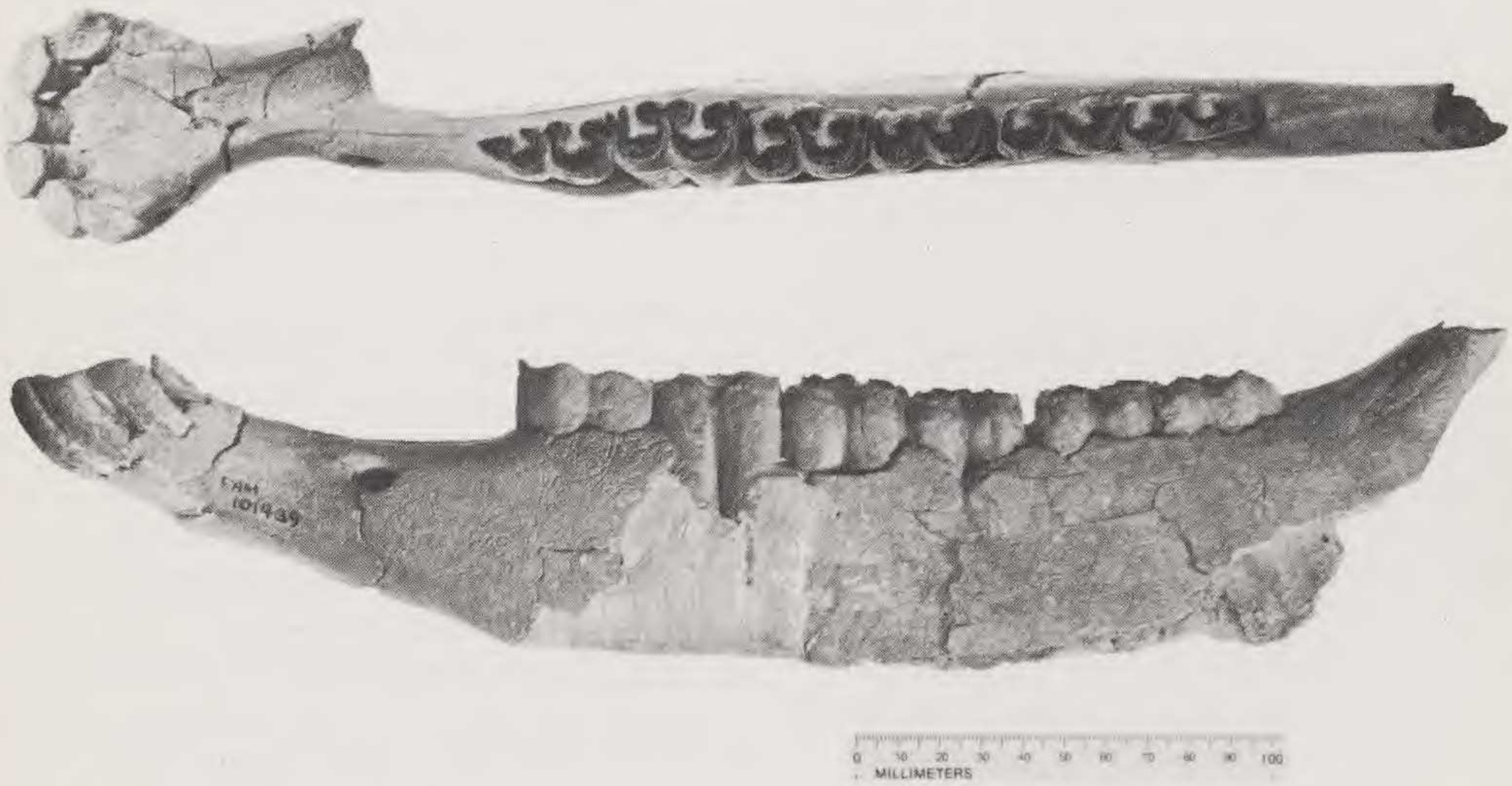


Fig. 5.
Occlusal and lateral photographs of symphysis and left ramus of *Hippidion* sp., F:AM 101439, from the Early Hemphillian of the Texas High Plains.

Genus ***Hippidion*** Owen, 1869

Revised Distribution. Early Hemphillian (Late Miocene) of Texas, Irvingtonian (Late Pliocene to Early Pleistocene) of California, and Late Pliocene to Pleistocene of South America (Sefve, 1912; Hoffstetter, 1952; Webb, 1976; this report).

Generic Diagnosis. Horses with nasal notch that lies above M^1–M^2. Nasal bones not retracted and they remain elongate splints. Dorsal lacrimal and ventral malar fossae absent. Incisors with cement-filled cups. Protocone oval with weak preprotoconal groove and well-developed postprotoconal valley. Lower cheek teeth with deep ectoflexids in the pre-

molars and molars. Enamel plications usually more complex than in *Onohippidium*. Monodactyl metapodials. For diagnostic characters not represented in specimens discussed in the present report, see Burmeister (1875), Sefve (1912), and Hoffstetter (1952).

Hippidion sp.
Figs. 5, 6, Table 1.

Referred Specimen. F:AM 101439, left ramus and symphysis with R I_3–I_1, L I_1–M_3.
Locality and Age. The Frick field crew of 1941 collected this specimen from unnamed rocks of the Ogallala Group, 10 miles north of Higgins, Lipscomb County, Panhandle of Texas (Tedford, personal communication, 1976; see Fig. 3). The fauna from this locality is undescribed, but it is similar in age to the Arnett l.f. from adjacent Oklahoma described by Kitts (1957). It is stratigraphically below the Higgins l.f. described by Hesse (1940). Tedford et al. (in press) consider the age of this locality to be Early Hemphillian (Late Miocene).
Description. I_1 and I_2 have cement-filled cups exposed at the occlusal surface (Fig. 5). I_3 has cups recessed below the occlusal surface. There is no precanine diastema and C is closely appressed to I_3. Sexual dimorphism is pronounced in fossil horse populations and the small canine size in F:AM 101439 indicates that this individual is a female. Posterior to the symphysial dentition the ramus is laterally constricted for the length of the postcanine diastema, which measures 69.6 mm from the posterior base of C to the anterior base of P_2. The mental foramen is approximately midway between C and P_2. The P_1 and its alveolus are absent.
The molars are narrower transversely than the premolars. The dental pattern of F:AM 101439 (Fig. 6) is similar to that of *Hippidion* illustrated by Burmeister (1875). P_2 is triangular-shaped and similar in dental pattern to the rest of the molars except for the addition of the anteriormost conid, which is characteristic of the P_2 in horses, whereas P_3 through M_3 have an anterointernal paralophid. The protoconid and hypoconid are exteriorly convex. The ectoflexid is relatively deep in the cheek teeth of F:AM 101439; this character is also seen in other *Hippidion* such as those described by Burmeister (1875), Sefve (1912), and Hoffstetter (1952). When the ectoflexid is very deep it subdivides the isthmus into the antroisthmus and postisthmus (Skinner, MS). The metaconids and metastylids are rounded and subequal in size for a given tooth. There is variation in the metaconid-metastylid complex within the tooth row.

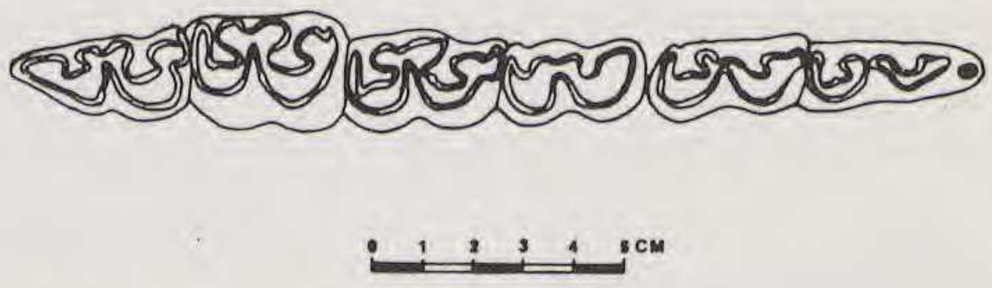


Fig. 6.
Occlusal view of *Hippidion* sp., F:AM 101439, showing details of dental pattern (see Fig. 5).

In P_2–P_4 and M_2–M_3 the metaconid is joined to the protolophid by a constricted antroisthmus and the metastylid is joined to the hypoconid by the postisthmus. In M_1 the isthmus is not as constricted as in the other teeth and the metaconid-metastylid complex is smaller and more poorly defined than the other molars. This variation in dental pattern of M_1 is probably a result of differential tooth wear. In the premolars, the hypoconid and entoconid are separated by a constriction. These same parts are less distinct in the molars. In the M_3, posterior to the hypoconulid, there is an isolated conid that is also seen in other *Hippidion*. This conid connects to the hypoconulid during later stages of wear. F:AM 101439 is similar in size to the smaller South American *Hippidion* species. For dental and size differences, Figures 4 and 5, and Table 1 should be compared to the illustrations and measurements of Burmeister (1875), Sefve (1912), and Hoffstetter (1952).
Discussion. The dental characters of F:AM 101439, especially in the diagnostic deep ectoflexids in both premolars and molars, present a convincing argument for its assignment

to *Hippidion*. The specific identification of the Texas *Hippidion* is best deferred to a study that incorporates other relevant specimens. The significance of this specimen with respect to the biogeography of South American "endemic" hoses will be discussed below.

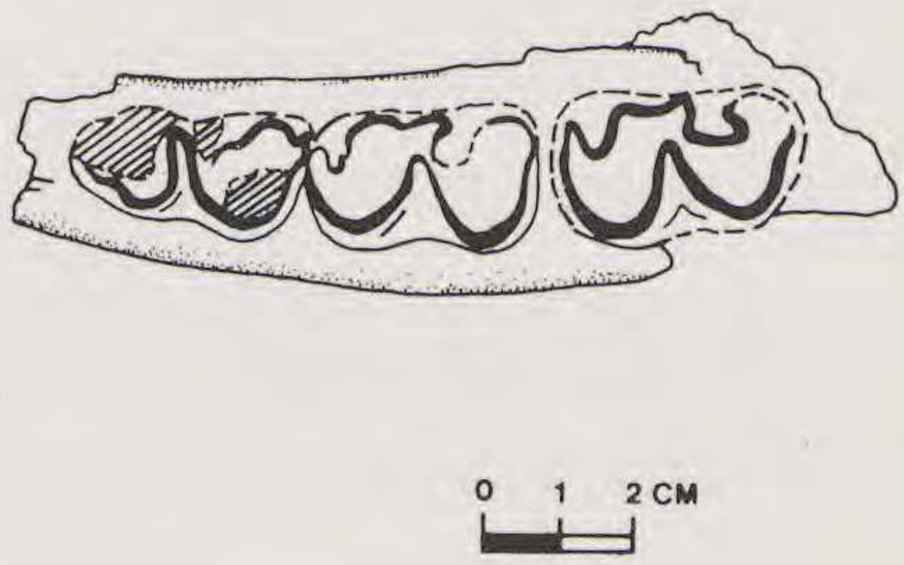


Fig. 7.
Occlusal view of cf. *Hippidion* sp., LACM 3363, ?P_3–M_1, from the Irvingtonian of southern California. Enamel is blackened for contrast. Broken areas are indicated by dashed lines (modified from an illustration prepared by Ms. F. Runyan of the LACM).

cf. ***Hippidion*** sp.
Fig. 7, Table 1.

Referred Specimen. LACM 3363, incomplete left ramus with fragments of three cheek teeth, probably P_3–M_1 (Fig. 7).

Locality and Age. This specimen was collected from LACM locality no. 1245–15 in sediments probably equivalent to the Vallecito Creek l.f. (Downs and White, 1965; Downs, personal communication, 1977). This local fauna occurs in the Matuyama reversed polarity epoch below a normal event that represents either the Réunion[1] or Olduvai. These constraints indicate an Irvingtonian (Late Pliocene to Early Pleistocene) age for the cf. *Hippidion* specimen that is bracketed by the Gauss-Matuyama boundary at about 2.4 million years ago and either the base of the Réunion event at about 2.1 million years ago or the base of the Olduvai event at about 1.85 million years ago (Lindsay, Johnson, and Opdyke, 1975; Opdyke et al., 1977).

Description and Discussion. LACM 3363 is very poorly preserved. The teeth, probably P_3–M_1, are less hypsodont than contemporary *Equus*. The dental pattern shows deep ectoflexids in both the premolars and molars, and, therefore, we refer this specimen to *Hippidion*. The principal importance of LACM 3363 is in the recognition of cf. *Hippidion* from Irvingtonian sediments of North America.

Biogeography

The origin of the South American "endemic" horses has been a matter of some interest in the past. Many students of fossil mammals, including Matthew (1924) and Stirton (1940), have recognized that this group was of North American origin. Horses are not found in South America until the Uquian (Late Pliocene to Early Pleistocene), roughly 2 million years ago (Marshall et al., 1977), and their appearance represents dispersal from North America during the opening of the Central American land bridge (Webb, 1976). Reed (1950, p. 76–77), in his discussion of the Milk Creek l.f. of Arizona, states that: "The horses appear to be related to *Pliohippus* [*Dinohippus*], and it has been suggested by Dr. R. A. Stirton of the University of California that they may be ancestral to the South American *Hippidium* [sic] of the Pleistocene." The great "morphological distance" between these North and South American horses has given rise to speculation as to structural and phylogenetic intermediates. Stirton (1940, p. 192) states that: "Upper Pliocene representatives of this group, when found, should display a moderately restricted narial notch in contrast to the extreme observed in *Hippidium* [sic]." As predicted by Stirton, morphologically intermediate forms are now known from North America as a result of the present report.

[1]The existence, duration, and boundaries of the Réunion event are presently uncertain (see, e.g., Opydke, 1972, and Watkins, 1972).

Table 1.

Tooth measurements (mm) for *Hippidion*.

	Hippidion sp., F:AM 101439												
	R I_3	R I_2	R I_1	L I_1	L I_2	L I_3	L C_1	L P_2	L P_3	L P_4	L M_1	L M_2	L M_3
A–P	11.8@	11.0	10.6	11.3	11.2	12.8@	3.2@	31.2	28.0	27.8	24.6	27.2	28.0
T	11.9	14.6	12.5	12.4	13.8	11.5	4.3	14.0	16.4	15.9	12.4	12.0	11.4

	Cf. *Hippidion* sp., LACM 3363		
	L P_3	L P_4	L M_1
A–P	30.2	28.4	27.6@
T	15.5	17.6	16.9

Abbreviation: @ = approximate.

As presently recognized, the one-toed horses include the genera *Pliohippus s. 1.* (including *Astrohippus*), *Dinohippus*, *Onohippidium*, *Hippidion* (including *Parahipparion*), and *Equus s. 1.* The phylogenetic relationships of these genera have not been dealt with adequately even in the classic studies of Sefve (1912), Osborn (1918), Stirton (1940), and Hoffstetter (1952). In fact, it might be shown that the taxon "one-toed horses" is not a strictly natural, i.e., monophyletic group. Based on the limited sample discussed in this report, we feel that a discussion of the interrelationships of *Onohippidium*, *Hippidion*, and other one-toed horses should be deferred to a more comprehensive study.

The major significance of the present study is in the biogeography of *Onohippidium* and *Hippidion* in light of the specimens described here. The time of differentiation of *Onohippidium* and *Hippidion* from their closest relatives has not previously been discussed. It has been implied that diversification obviously occurred either in North America before dispersal southward or in South America after dispersal southward. We conclude that: 1) Clearly differentiated forms of *Onohippidium* and *Hippidion* are found in Hemphillian (Late Miocene to Early Pliocene) deposits of North America. 2) These genera subsequently dispersed to South America apparently during the Pleistocene faunal interchange. 3) Cf. *Hippidion* sp. is also found in Irvingtonian sediments in North America.

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